



Historical trends and future distribution of anchovy spawning in the Bay of Biscay

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ABSTRACT

Future scenarios of fish stocks and the impacts of climate variability and change on fisheries are critical to anticipate and minimize potential economic losses in this sector. In this study, we assessed the impact of recent sea warming and future climate change on anchovy in the Bay of Biscay, where sea surface temperature has increased in the last three decades. We analyzed the historical evolution of the anchovy spawning and built species distribution models that are projected under the RCP8.5 climate change scenario. The historical analysis of anchovy spawning showed that spawning peak advanced at a rate of 5.5 days/decade from 1987 to 2015, and the gonadosomatic index (as proxy of spawning activity) generally increased, which might be associated to changes in phytoplankton abundance. In addition, the spawning area expanded and contracted depending on the total egg production. In the future, the overall anchovy egg abundance in the Bay of Biscay is expected to increase between 1.05 and 2.66-fold under the RCP8.5 climate change scenario by the mid and end-of-the-21st-century, respectively. Projected environmental changes are expected to induce an expansion of the spawning area (7.8% and 16.4% for mid- and end-of-the-century) and higher egg densities.

1. Introduction

Global climate change is unequivocal and since 1950, atmospheric and oceanic temperatures have risen steadily (IPCC, 2013; Rhein et al., 2013). Temperatures in the upper layers of the ocean (0–75 m) have shown an increase of $0.11 \pm 0.02^\circ\text{C}$ per decade over the period 1971–2010, causing an increase of 4% in stratification (IPCC, 2013; Rhein et al., 2013). Climate change has a significant impact across all marine ecosystems, latitudes and trophic levels (Cheung et al., 2013; Poloczanska et al., 2013). As a response to ocean warming, species shift biogeographic ranges and/or alter phenology (seasonal biological phenomena in relation to climatic conditions) to accommodate temperature changes and maintain their thermal niches (Poloczanska et al., 2013; Richardson et al., 2012). A poleward migration of geographical boundaries of different marine species is expected with an increase in the catch potential in high latitudes and a decrease in many tropical and subtropical regions (Cheung et al., 2009). Some warm water fish species have been reported to be expanding their northern distribution limits

and accelerating the general latitudinal movement detected for past decades, e.g. Atlantic mackerel (*Scomber scombrus*), Atlantic cod (*Gadus morhua*), bib (*Trisopterus luscus*), blue whiting (*Micromesistius pou-tassou*), Norway pout (*Trisopterus esmarkii*) and scadfish (*Arnoglossus laterna*) (Beare et al., 2004; Bruge et al., 2016; Lenoir et al., 2011; Montero-Serra et al., 2015; Perry et al., 2005). Substantial local population extinctions are projected by 2050 under climate change scenarios, particularly in subpolar and tropical regions and semi-enclosed seas such as the Mediterranean Sea (Cheung et al., 2009).

Small pelagic fish dynamics are often related to environmental fluctuations (Borja et al., 2008; Checkley et al., 2009) and respond rapidly to climate variability (Montero-Serra et al., 2015). Therefore, they can be good biological indicators of climate-driven changes in marine ecosystems (Peck et al., 2013). The European anchovy (*Engraulis encrasicolus*, Linnaeus 1758) is a small pelagic fish with fast growth, high mortality and fecundity (Motos, 1996) and a short life cycle with a maximum lifespan of 4 years (Motos, 1996; Petitgas et al., 2012; Uriarte et al., 2016). This species is distributed across the eastern North and

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Central Atlantic and range from NW Africa in the south to the North Sea and the Baltic Sea in the north including Mediterranean Sea, Black Sea and Azov Sea (Reid, 1966). European anchovy presents a wide distribution but with differentiated populations often related to local features such as upwellings, bays and estuaries (Zarraonaindia et al., 2012). One of these populations is located in the Bay of Biscay (BB). This anchovy population selects stable habitats related to river plumes, with the Adour and Gironde estuary zones constituting key areas (Koutsikopoulos and Le Cann, 1996; Sagarminaga et al., 2004), and shelf edge fronts and oceanic eddies due to their higher primary production (Motos et al., 1996). The anchovy spawning peak generally occurs during a period of rapid environmental changes. This peak can be initiated by changes in daylight, changes in winds, decreases in freshwater runoff, or warming of atmospheric and sea water temperatures (which vary between 12 °C at the end of winter and 20 °C at the beginning of summer in the BB) (Koutsikopoulos and Le Cann, 1996; Sanz and Uriarte, 1989). The spawning season occurs between March and August (Motos, 1996) starting in the southeast and moving gradually north- and westward (Planque et al., 2007). There are two different spawning areas: coastal and oceanic (Motos, 1996; Uriarte et al., 1996). Coastal spawning areas are characterized by a high primary production, strong stratification and stability influenced by river plumes. Anchovy spawning in these areas are small, mostly 1-year-olds (Ibaibarriaga et al., 2013; Sagarminaga et al., 2004; Uriarte et al., 1996). The oceanic spawning areas, which are along the continental slope and have no influence of continental fresh waters (Uriarte et al., 1996), are used by bigger and older anchovies to spawn (Motos, 1996; Uriarte et al., 1996). The spawning timing is different for young and older adults. In April, the larger/older anchovy start to spawn and are followed by smaller/younger anchovy which prefer slightly higher temperatures (Lucio and Uriarte, 1990). The peak of the spawning activity (when most fish present are actively spawning) occurs in May (Sanz and Uriarte, 1989), and it is associated with temperatures between 14 and 18 °C (Montero-Serra et al., 2015; Motos et al., 1996; Portner and Peck, 2010; Sagarminaga et al., 2004).

In the Bay of Biscay, the sea surface temperature warmed at a rate of 0.26 ± 0.03 °C per decade between 1982 and 2014 (Costoya et al., 2015), having differential seasonal rates of change (faster decrease from September to November than warming from April to June). The duration of the warm season (period between first and last day in which sea surface temperature exceeded the 75th percentile temperature) increased between 6 and 14 days per decade on average (Costoya et al., 2015). As a response to this sea warming, changes in the abundance of some fish were observed during the last decade of the 20th century and first decade of the 21st century (Poulard and Blanchard, 2005), but have not been reported for the BB anchovy population. We hypothesize that changes in phenology and abundance of the BB anchovy population might have occurred in the last few decades or are expected in the future in response to these environmental variations.

The main objective of this study is to assess the effect of recent sea warming and the impact of climate change on the spatio-temporal spawning distribution of anchovy in the Bay of Biscay. Specific objectives are: 1) to analyze trends in the distribution and phenology of the anchovy in the Bay of Biscay and to identify the main ocean-climatic factors determining the spawning of this species; 2) to build a species distribution model of anchovy egg abundance based on its ecological niche; and 3) to project the distribution model under climate change scenarios to assess expected changes in its abundance.

2. Material and methods

2.1. Study zone

The study zone is the Bay of Biscay (BB), an open oceanic bay located in the northeast of the Atlantic Ocean (Fig. 1). It has a complex hydrological regime and weather pattern, both of which show spatial

and temporal heterogeneities (Costoya et al., 2015; Koutsikopoulos and Le Cann, 1996; Valencia et al., 2004). The BB is characterized by an average weak ocean circulation, the presence of cyclonic and anticyclonic eddies, a poleward flow along the slope driven by wind and density gradients, tidally-induced currents over the continental shelf, and freshwater runoff and river plumes formed in the mouth of the Gironde and Loire estuaries (Koutsikopoulos and Le Cann, 1996). The sea surface temperature shows a latitudinal gradient during the summer period and important freshwater runoffs from the Adour and Gironde estuaries (Koutsikopoulos and Le Cann, 1996; Valencia et al., 2004).

2.2. Biological data

Two sources of data for the European anchovy population of the Bay of Biscay were used in this study. On the one hand, egg and adult data have been collected annually during the BIOMAN surveys (BIOMass of Anchovy, Santos et al. (in press)) between 1989 and 2015 (Fig. 2). The objective of these surveys is the estimation of the spawning stock biomass by applying the Daily Egg Production Method (DEPM) (Lasker, 1985) and improving the knowledge of the spawning environment (Santos et al., in press). On the other hand, additional adult biological samples have been collected annually from the commercial catches landed in the Basque Country during the fishing season from the same time series.

2.2.1. Anchovy eggs data

BIOMAN surveys were carried out between May and the first half of June, to coincide with the peak of the spawning period. The area covered by BIOMAN was the wide French continental shelf-oriented S-N from 43.30° to 47.88° N, and the narrow Spanish shelf-oriented E-W from 1.22° to 7.78° W which corresponds to the main spawning area of anchovy (Fig. 1). Limits of the sampling zone varied between years and the criteria for defining them is a continued absence of eggs in consecutive sampling stations. Sampling stations were located every 3 nautical miles (nm) along transects perpendicular to the coast and separated 15 nm. The adaptive sampling method is helped by the use of near-real time sampling with CUFES (Continuous Underway Fish Egg Sampler, Checkley et al., 1997) explained in Santos et al. (in press) and was routinely applied along vessel tracks each 1.5 miles at 3 m depth aside the deck. In areas of high egg abundances or where historically high egg production have been found (as in the river plumes), additional transects separated by 7.5 nm were completed. This led to gain in precision (i.e. reducing variance) regarding egg counts and more detailed egg spatial distribution. Following the same criteria, distance between stations along transects changed from 3 to 6 nm when eggs were absent, particularly when moving towards offshore areas. A vertical plankton haul was used for egg sampling, using a CALVET type “PairoVET” net with a 150 µm mesh (Smith et al., 1985). The maximum sampled depth was 100 m, or 5 m above the sea bed in shallower waters. The net was equipped with digital flowmeters (G.O. 2030) for determining the amount of water passing through the net (Santos et al., 2011). A total of 13,732 PairoVET hauls were conducted between 1989 and 2015. At the end of collection, plankton samples were preserved immediately in 4% formaldehyde buffered with sodium tetraborate and after 6 h fixation, all eggs were sorted out on board. Anchovy eggs, which are easily distinguished by their characteristic oval shape, were identified and counted. The number of eggs per haul were converted to density (eggs m⁻²) using flowmeter readings and maximum sampled depth (Smith and Richardson, 1977).

To study the spatial and temporal distribution of anchovy eggs, abundance values for each 0.1° × 0.1° resolution squares were estimated. For that purpose, the arithmetic means of values for each square were calculated. The data were analyzed in two forms: Presence/Absence (PA, 1 = presence, 0 = absence, binomial form) and Density (ED, eggs m⁻²), with logarithmic transformation.

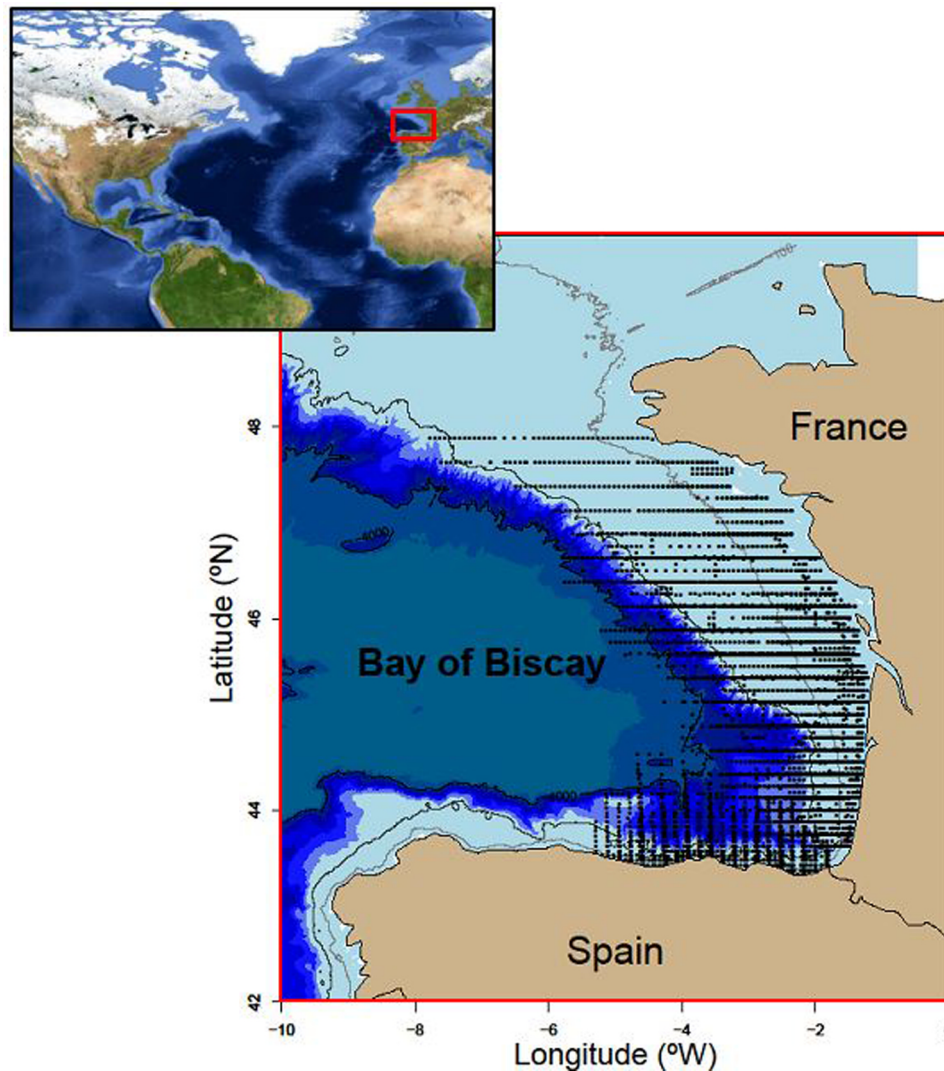


Fig. 1. Study area and stations of the vertical hauls (PairoVET) that could be performed during the surveys (Santos et al., in press). Bathymetry with 100, 200 and 4000 m isobaths are also represented.

2.2.2. Anchovy adult data

The information on adult fish was provided from: i) pelagic trawls carried out at the same time as the anchovy egg sampling during BIOMAN surveys, with size, weight, sex and age data recorded between 1990 and 2014, with gaps in 1993 and 1996, and ii) ANEBIO (ANchovy BIOlogical data) dataset, collected using samples of commercial anchovy catches from which length, weight, gonadal weight, sex, maturation and age were recorded between 1986 and 2015 (without information for 2004 and between 2007 and 2009 due to the closure of the fishery) (Fig. 2).

2.3. Environmental data

Oceanographic data from BIOMAN sampled stations were collected using a CTD (Conductivity, Temperature and Density) profiler. The variables used for modelling were sea surface temperature (SST, which was recorded at each station), and sea surface salinity (SSS, recorded at every third station in the first year and every station thereafter). A re-analysis of environmental data was also used to extrapolate the model to the entire Bay of Biscay. With those environmental data, we were able to model with higher spatial resolution in shallow coastal waters, where global climate models are inadequate (Richardson et al., 2012). The Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis data (a. k. a.

NEMO reanalysis) use the NEMO model for the period 2002–2014 with a $1/12^\circ$ spatial and monthly temporal resolution. Variables used were SST, SSS, and Mixed Layer Depth (MLD) averages for May and June. Monthly means and standard deviations were calculated for BIOMAN and NEMO reanalysis data to estimate the variation between the two sources and ensure that we were not introducing noise in the model (Suppl. Info. Table 1). BIOMAN SST and SSS data were used as the environmental conditions of the spawning period peak to build the model. For the projection to the Bay of Biscay, we used the NEMO reanalysis environmental data. May and June averaged chlorophyll-a (chl-a) concentrations were used as a proxy for phytoplankton abundance. These data were sourced from various satellite sensor data sets (SeaWiFS, MODIS, MERIS and VIIRS) between 2002 and 2014 (available from GlobColour at <http://hermes.acri.fr/>) and with 4 km spatial resolution. Bathymetry data from NOAA database was extracted using the 'marmap' R package (Pante and Simon-Bouhet, 2013) with $0.1^\circ \times 0.1^\circ$ spatial resolution.

NCEP Global Ocean Data Assimilation System (GODAS) data for a $0.333^\circ \times 1^\circ$ latitude-longitude grid between 1989 and 2015 were also used to relate with biological indices. A bilinear interpolation was performed to obtain higher resolution grid ($0.5^\circ \times 0.5^\circ$) (Brüge et al., 2016).

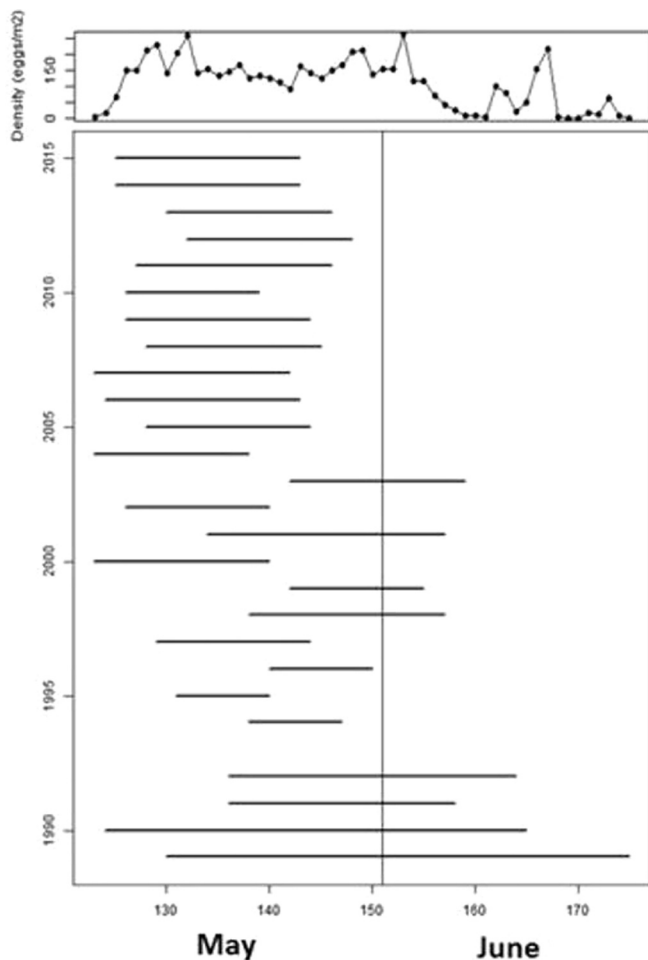


Fig. 2. BIOMAN survey times for different years and egg density (egg m⁻²) average for each Day of the Year.

2.4. Gonadosomatic index (GSI) and yearly peak of the spawning period

The Gonadosomatic index (GSI) is an indirect approach to evaluate the reproductive status of fish (Brewer et al., 2008) and has been used as an indicator of reproductive activity and peak spawning periods (Kreiner et al., 2001). GSI, a ratio of gonad weight to total body weight, was calculated using the equation of Bougis (1952):

$$GSI = \frac{\text{Gonad weight}}{\text{Total body weight}}$$

The GSI was computed only for female individuals collected from BIOMAN and ANEBIO described above and some measurements were removed based on the maximum values of length reported in Fishbase (200 mm, <http://www.fishbase.org/>). Data for January, February, October, November and December were not included in GSI trend analysis due to the low number of samples. Data from year 1986 were also discarded, because of the scarcity of samples. The logarithm of the Gonadosomatic index was modeled by means of a Generalized Additive Model (GAM, Wood, 2017) as a function of an interaction between the day of year (D) and year (Y) (to be able to analyze the phenology changes throughout years) and total anchovy length (L) (due to the correlation between the size and spawning capacity of the anchovies):

$$\log(GSI) \sim te(D, Y) + s(L),$$

where te is a tensor product that represents the interaction between D and Y, which is forced to be cyclic for D, and s is a smooth function. We used 'mgcv' package implemented in R language (Wood, 2017) for this purpose. Using predicted GSI data from the model, the spawning peak

was calculated as the Day of the Year with the maximum GSI value and the duration was estimated as the time between the days of the year when the fitted GSI values of the curve exceeds 0.036, a threshold for which individual anchovy females are mature with a 99% certainty (from an ad hoc maturity logistic model fitted to the DEPM survey data based on histological analysis). The spawning peak, duration of the spawning and the maximum GSI value trends were evaluated, excluding years without monthly data, i.e. 1999, 2000 and 2007. The correlation with different environmental variables which could potentially affect the timing of spawning peak was analyzed. Yearly anomalies for the average of the months prior to the spawning peak (February–May) were estimated for SST, SSS, MLD and Chl-a as a proxy of phytoplankton.

2.5. Spawning distribution models

Anchovy egg distribution in the Bay of Biscay was modeled using Generalized Additive Models (GAMs) based on the method described in Bruge et al. (2016) for mackerel (*Scomber scombrus*) in the North East Atlantic. Egg Presence/Absence (PA) and Density (ED, for non-zero observations) were modeled separately and subsequently combined following the methodology described in Borchers et al. (1997) for horse mackerel (*Trachurus trachurus*):

1. The first step was to fit the PA model using the presence/absence of anchovy eggs as a response variable and a binomial error distribution with a logit-link function. *Dredge* function of 'MuMin' R-package was used to generate a set of models with combinations (subsets) of terms in the global model (Barton, 2016), with rules for model inclusion based on lowest AIC (Akaike Information Criterion), which means a better fit (Bruge et al., 2016; Guisan and Zimmermann, 2000; Sakamoto et al., 1986). The confusion matrix accuracy assessment (VanDerWal et al., 2012) was also used to evaluate how reasonable was the discrimination of the presences from the absences through sensitivity (true predicted presences) and specificity (true predicted absences) estimation. The occurrence probability was converted to Pres/Abs by adjusting the threshold obtained using an optimization method based on the maximization of sensitivity plus specificity criteria (Jiménez-Valverde and Lobo, 2007). Overall accuracy provides the proportion of either true positive or true negative predictions.
2. The second step was to fit the egg density model using log-transformed ED as a response variable and Gaussian error distribution only on squares where there were anchovy eggs. We used the same variable predictors selected in the PA model. Predicted ED was conserved in the final model only if it was predicted as a presence in the PA model. In the case of the PA model predicting an absence of eggs, ED would be 0.
3. The last step was the validation of the constructed Presence/Absence model using cross-validation resampling method (Burnham and Anderson, 2003). This method is based in the division of datasets (in k equally sized groups following the k -fold partitioning method (Hijmans et al., 2013)) which are used to fit the model and the subsequent validation. We used $k = 5$ in order to use 80% of randomly selected observations to fit the model and the remaining 20% to validate it. Accuracy, which provides the proportion of either true positive or true negative predictions, was calculated by comparing predictions against observations with the R-squared. This value was compared with the overall explained deviance and a large difference between both values would indicate overfitting.

2.5.1. Spawning reconstruction model (1989–2015)

To analyze the trends between 1989 and 2015 in spawning and disentangle the potential drivers, a spawning distribution model using only spatio-temporal variables was built following the steps defined previously. The spawning reconstruction model was built in order to

avoid bias in species distribution due to a non-uniform distribution of sampling in space and time (Bruge et al., 2016; Chust et al., 2014). The predictors used were: year (to reconstruct the temporal pattern), log-transformed bathymetry (LogBathy, as a descriptor of geographical attachment to the continental shelf) and latitude (as spatial term) (Bruge et al., 2016). The population center of gravity (as the mean location of the individuals that compose the population (Bez and Rivoirard, 2001), in this case of the total egg density) and 5% and 95% percentiles (P5 and P95, estimated as weighted quantiles) were calculated to identify the main drivers on the position of the gravity center. P95 gives essential information of the anchovy eggs distribution because the Bay of Biscay is limited by land in the south and east. SST trends for May and June and the average of both months (as the proxy of the temperature in the peak of spawning) were also evaluated, considering the averaged boundaries of the spawning area. Another driver analyzed was density-dependent population dynamics. To address this, the correlation between the gravity center latitude and the total daily egg production estimated from the DEPM (Santos et al., in press) for each year was calculated.

2.5.2. Spawning niche model

With the aim to analyze the current spawning niche of the Bay of Biscay anchovy population, a model including environmental variables was built following the same steps as in the reconstruction model. Individual GAMs were previously built in order to analyze the response curves and the deviance explained of the anchovy eggs by different environmental variables (Thuiller et al., 2004). GAMs were built for BIOMAN and NEMO reanalysis-SST and SSS (for which each point we have a measure of the variable), for NEMO reanalysis-MLD, for Hermes chlorophyll-a concentration and NOAA bathymetry, as well as log transformed data for the last two variables (LogChla and LogBathy). In order to fit unimodal response curves and avoid overfitting (according to the ecological niche concept), degrees of smoothness (“k” values) were set equal to or less than 3 (Burnham and Anderson, 2003; Hastie and Tibshirani, 1990). BIOMAN environmental data were used for building individual GAMs between anchovy eggs densities and environmental variables, and for the validation of the model. For the extrapolation of the model, NEMO reanalysis environmental data were used. Raw data for anchovy eggs were also represented to compare modeled and observed egg distribution patterns.

2.6. Future projections under climate change scenarios

Using the spawning distribution model built in the previous step, future projections for the anchovy population were conducted for the mid (2040–2059) and the end-of-the-21st-century (2080–2099) under the RCP8.5 scenario of the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC5). RCPs (Representative Concentration Pathways) are greenhouse gas concentration trajectories. The RCP8.5 is the highest-carbon-emission scenario (936 CO₂ ppm by the end of the century), which prescribes a continuous increase in greenhouse emissions that results in a 2.6–4.8 °C global atmospheric warming and a ~2 °C ocean surface warming (top 100 m) by the year 2100 (IPCC, 2014). Projections of oceanographic variables (SST, SSS, and MLD) under RCP8.5 were extracted from two sources: 1) the Max Planck Institute's Ocean Circulation Model

Table 2

Deviance explained in % for different variables in PA (presence/absence) and ED (log transformed density) models. *n* is the number of samples used in the model.

Variables	GAMs	PA (%)	LogED (%)	n
SST (BIOMAN)	s (SST, k = 3)	23.50	25.00	1020
HR SST	s (HRSST, k = 3)	19.20	28.80	1171
SSS (BIOMAN)	s (SSS, k = 3)	10.60	15.40	887
HR SSS	s (HRSSS, k = 3)	9.36	14.70	1171
HR MLD	s (HRMLD, k = 3)	20.80	27.50	1171
Chlorophyll-a	s (Chla, k = 3)	1.77	3.40	1202
Log(Chla)	s (LogChla, k = 3)	2.05	3.17	1202
Bathymetry	s (Bathy, k = 3)	4.13	7.11	1175
Log(Bathy)	s (LogBathy, k = 3)	6.00	9.00	1175
Lat	s (Lat)	6.08	8.30	1202
Long	s (Long)	31.4	43.20	1202
Lat, Long	s (Lat,Long)	41.1	55.30	1202

(MPIOM) with a 0.5° x 0.5° spatial and monthly temporal resolution (Tables 1, 2) the average of 16 IPCC5 models that contain a biological module (hereinafter Ensemble) with a mean ~1° spatial resolution (Cabr   et al., 2014). For the IPCC Ensemble, only end-of-the-century projections are studied, e.g. differences between years (2080–2099) and (1980–1999). Note that the resolution along coastal zones is low in both projections. The global sea surface temperature increase calculated as the average of these 16 IPCC5 climate models is 2.51 ± 0.59 °C (Cabr   et al., 2014). Chl-a was not used as a variable in future anchovy egg modelling because of the low correspondence between its distribution in biogeochemical models at the reference period and that of NCEP reanalysis.

The niche-based model used 2006–2020 data as the reference period and 2080–2099 as the end-of-the-century period and 2040–2059 for mid-century. Future ocean boundary forcing are created by adding a change in different variables to simulated present day forcing (Holt et al., 2010; Tinker et al., 2016). Different parametrizations in the formulation of the models could have, as a consequence, biases between present climate simulations and reanalysis or observations and also in future climate model simulations (Zahn and von Storch, 2010). Many methods were proposed to overcome this issue, but a common simple method often used is the so called “Delta method” (Holt et al., 2010; Zahn and von Storch, 2010), which is based in a constant shift of the mean, maintaining present observational distributions. The expected effect of climate change was calculated as the difference between the averages in 2080–2099 (or 2040–2059) and 2006–2020 for each variable. Subsequently, this average difference was added to each grid cell in the NEMO reanalysis variable. Therefore, future projections of climatology are estimated based on historical climatic conditions (observations between 2002 and 2014) and change signal (delta) as follows:

$$\text{Future projections}_{(2080-2099)} = \text{Historical conditions}_{(2002-2014)} + \text{Delta},$$

where

$$\text{Delta} = \text{RCP8.5}_{(2080-2099)} - \text{Reference conditions}_{(2006-2020)}$$

The spawning niche model was then applied to the reference and the future periods, which were compared by means of a difference

Table 1

Different change delta values ± standard deviation estimated for the Bay of Biscay used to get future environmental conditions. SST in °C, SSS in psu and MLD in meters.

	Mid-of-the-century (2040–2059)			End-of-the-century (2080–2099)		
	SST	SSS	MLD	SST	SSS	MLD
MPIOM	0.52 ± 0.28	− 0.30 ± 0.13	− 7.48 ± 8.31	1.51 ± 0.71	− 0.57 ± 0.35	− 12.40 ± 12.84
Ensemble				2.27	− 0.59	− 35.83

between the two periods. Additionally, individual-variable models were conducted to analyze which variable triggers the main change in egg density and distribution by the end of the century.

2.7. Comparison between the center of gravity (CoG) for past and future

The CoG was used to evaluate the impacts of climate change on the anchovy spawning distribution. A comparison between the CoG in future projections under RCP8.5 conditions and present was also conducted. Annual latitude and longitude locations of the percentiles 5% (P5) and 95% (P95) of the egg density (ED) were also computed and variation rate was estimated in kilometers per decade. To estimate the overall ED, we summed the ED of the whole BB (for both present and future projections) and used it as a proxy of total egg production. Thus, we estimated the ED difference between end-of-the-century conditions and present conditions.

3. Results

3.1. Changes in spawning between 1987 and 2015

3.1.1. The Gonadosomatic index and the relationship with environmental variables

The Gonadosomatic index (GSI) showed a rapid increase between March and May and a decrease at a slower rate from May to September (Fig. 3). The peak of spawning was in May with GSI greater than 0.08 (8% of the body weight corresponding to gonads), whilst outside of the spawning period (i.e. end of August to March) these values did not exceed 2% on average (Fig. 3). The fitted GAM of the GSI shows two peaks (around 1993 and 2010) with a general increasing temporal trend (Fig. 4). Predicted GSI curves showed differences between years in both, amplitude and duration (Fig. 5). The peak of the spawning advanced significantly (p -value < 0.001) at a rate of 5.5 days per decade with the main change between 2003 and 2015 (Fig. 6). Beginning and end of the spawning period also showed changes with time. Until 1998 the spawning period became longer (started earlier and finished later). From then until 2006, the spawning period decreased to similar values as at the beginning of the series but the end of the spawning period occurred later. From 2008 onwards there seemed to be a shift, with both the peak and the spawning period occurring earlier. The observed spawning peak occurs before the maximum of temperature and chlorophyll-*a* (Supp. Info Fig. 1a, d), after the main salinity peak but before the second one (Supp. Info Fig. 1b), and after the maximum of MLD (Supp. Info Fig. 1c). The correlation with a set of environmental variables which could potentially affect the timing of the spawning peak, only showed a significant negative correlation with chl-*a* (p -value = 0.04) and no correlation with SST (p -value = 0.25), SSS (p -value = 0.14) and MLD (p -value = 0.32). It means that when the anomaly of chlorophyll-*a* concentration is positive, the spawning peak anomaly is negative, i.e. occurs earlier in the year.

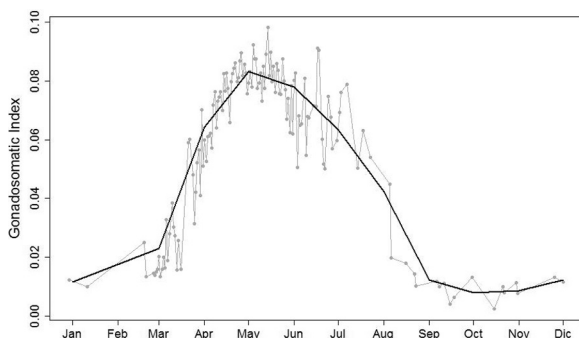


Fig. 3. Gonadosomatic Index means for each Day of the Year (grey line) and means for months (black line) calculated for time series years (1987–2015).

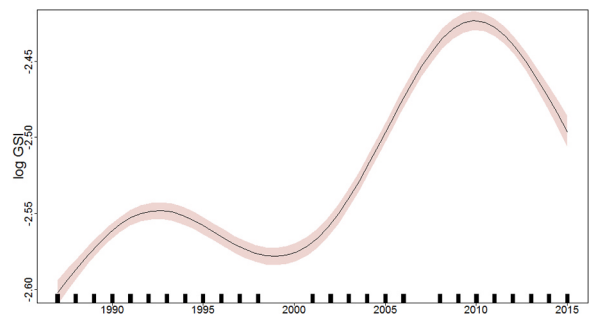


Fig. 4. Log-transformed GSI response curve through years.

3.1.2. Spawning reconstruction model (1989–2015)

Total egg production of the BB anchovy showed a large decrease between 2001 and 2005, when the stock collapsed and the fishery was closed (Fig. 7). After that, a rapid recover occurred until 2010, when the fishery was opened again. Total egg production did not show a statistically significant linear trend (p -value = 0.48) from 1989 to 2015. The spawning reconstruction model had AUC (Area Under the Curve), sensitivity and specificity of 0.73, 0.77 and 0.70, respectively. The P95 of the raw ED observations and the spawning spatio-temporal reconstruction model did not change significantly between 1989 and 2015 (p -value = 0.19 and 0.64, respectively, Fig. 8a). Sampling effort CoG in 2015 was 70 ± 35 km farther north than in 1989 and the north boundary (P95), 113 ± 56 km (Fig. 8b). The sampling effort CoG shift was found to be significant (p -value < 0.001) with an increase of 27.0 ± 1.33 km/decade. Both percentiles (5%, P5 and 95%, P95) shift northward in time (p -values = 0.0003 and 0.0008, respectively), with a northward shift limit of 43.8 ± 2.2 km/decade. However, the analysis of the anchovy egg abundance, showed a non-significant northward shift of 5.9 km/decade for the P95 in the reconstructed model and 18.1 km/decade estimated with the raw data.

Anchovy spawning latitudinal CoG and P95 were statistically correlated with total egg production (both p -value < 0.001, Fig. 9) but not with GODAS sea surface temperature. GODAS data sea surface temperature, showed a statistically significant increase of 0.59 °C between 1989 and 2015 (0.23 °C /decade, p -value = 0.04) over the period of May–June in the sampled area (Supp. Info. Fig. 2).

3.2. Spawning niche model

Environmental variables used for building the anchovy egg spawning distribution model after selection with dredge were SST, SSS, MLD, chl-*a*, and LogBathy. Different deviance explained can be seen in Table 2. Geographical position was also introduced in the model with a bivariate smooth (s (latitude, longitude)). The model with all these environmental variables explained 48.4% and 58.1% of the deviance for the PA and ED models, respectively. The Presence/Absence habitat model had an AUC, sensitivity and specificity of 0.835, 0.855 and 0.815, respectively. The R-squared of the egg density model cross-validation (46.5%) was close to the deviance explained (58.1%) therefore this model was not considered overfitted. Fig. 10 shows response curves from the PA (a) and ED (b) models, whilst Fig. 11a and b shows egg observations and habitat model or anchovy spawning distribution model in the present.

Different models were built (Table 3) and the total anchovy egg abundances were compared with mid- and end-century projections. In all those models, chl-*a* was excluded as previously explained. The model with all variables except chl-*a*, explained 48% (PA) and 57.8% (ED).

3.3. Projections of anchovy spawning under the climate scenario

Under the RCP8.5 climate change scenario, the MPIOM model

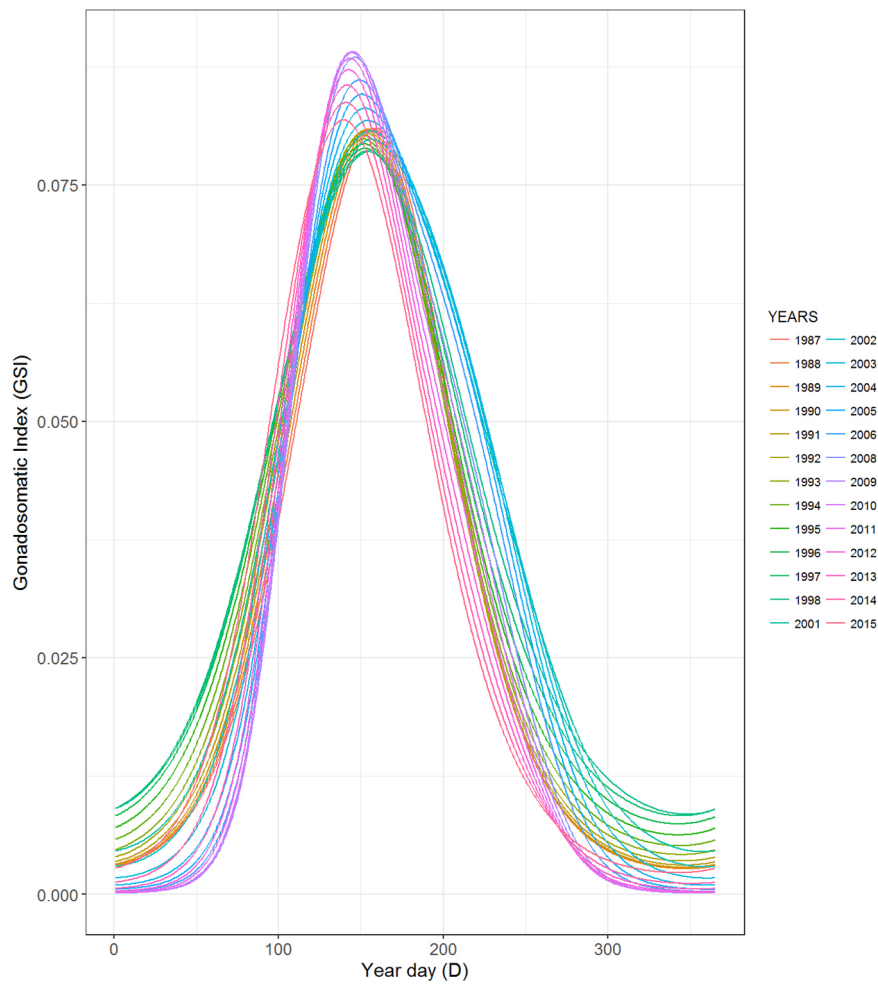


Fig. 5. Anchovy GSI yearly spawning cycle along time series (1987-2015).

projects the following changes in the spawning area for the mid (2040–2059) and end of the century (2080–2099) with respect to the present (2006–2020): an increase in SST of $0.52 \pm 0.28^\circ\text{C}$ and $1.51 \pm 0.71^\circ\text{C}$, a decrease in salinity of 0.30 ± 0.13 psu and

0.57 ± 0.35 psu, and a decrease in mixed layer depth of 7.48 ± 8.31 m and 12.40 ± 12.84 m, respectively. SST, SSS, MLD and log-transformed bathymetry were the chosen variables in the final model. Chlorophyll-a concentration was not selected in future models

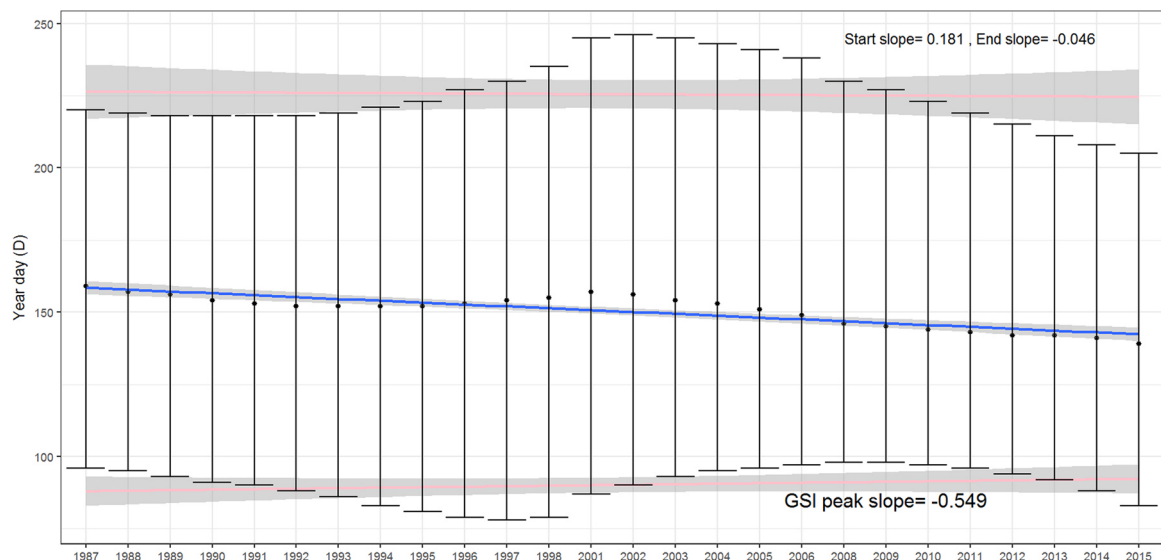


Fig. 6. Day of the Year when the beginning, the peak and the end of the spawning occur between 1987 and 2015. Smooth curves estimated for the beginning and the end (in pink) and peak (in blue) of the spawning period are also plotted.

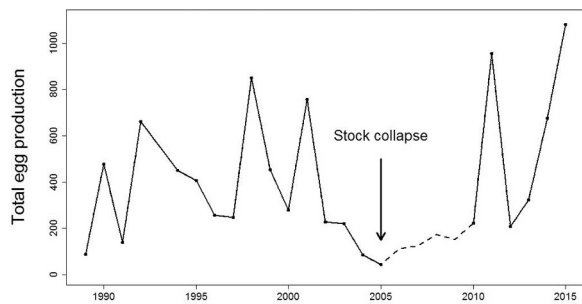


Fig. 7. The Bay of Biscay anchovy total egg production between 1989 and 2015 time series. Anchovy stock collapse and recover years when fishery was closed (in dotted lines).

due to the low resolution and reliability of the projections in coastal areas.

The density of anchovy eggs is projected to increase by mid-century (Fig. 11c) and to increase even more by the end-of-the-century (Fig. 11d). The highest abundances appeared close to the coast, associated with river plumes. However, an expansion of the spawning area occurred over time. It is predicted that there will be an increase in the spawning area of 7.8% (32,313 km²) and 16.4% (67,793 km²) for mid- and the end-of-the-century. Total egg abundance was predicted to be 1.57 times higher by mid-century compared to the present in the Bay of Biscay (rising from 80,076 eggs in the present to 125,984 in 2040–2059, Fig. 11b, c), and 2.66 times higher by the end-of-the-century (211,854 eggs in 2080–2099, Fig. 11b, d). The center of gravity (CoG) of the egg density is expected to shift 15.6 km southward and 6.5 km eastward by the mid-century and 24 km northward and 1.5 km westward by the end-of-the-century.

Three different models were considered by changing one by one the variables SST, SSS and MLS in order to explore which of the variables was the most influential with regards to future projections. SSS was found to be the variable that projected the highest increase in egg abundance. The total egg abundance in the BB projected by the SSS model increased by 1.27 (1.57) times the present value for mid- (end-of-the-century) (Supp. Info. Fig. 3c, d). The second most important variable was SST, which when projected as the sole variable, projected a 1.10 (1.43) times higher egg abundance (Supp. Info. Fig. 3a, b), whilst MLD projected the lowest abundance increase with 1.05 (1.09) times by mid- (end-of-the-century) (Supp. Info. Fig. 3e, f). Most areas predicted

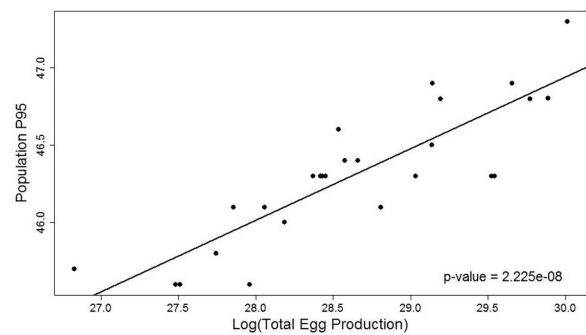


Fig. 9. Correlation between anchovy eggs distribution P95 (north boundary) and logarithm of the total egg production.

as suitable zones in the three models were found in river plumes (Adour, Gironde and Loire).

4. Discussion

4.1. Spawning seasonality and historical trends

The gonadosomatic index showed a strong seasonal pattern with a marked peak between May and June and a sexual resting period between September and February. Some individuals showed an early GSI increasing in March and all of them showed a decrease by September, being the spawning period between April and July–August (depending upon the year). The result is rather consistent with that of Sanz and Uriarte (1989), although in some years is longer as spawning may reach mid-August.

Phenology changes were found between 1987 and 2015 in BB anchovy, with an advance of 5.5 days per decade in the spawning peak. The duration and peak of the spawning period showed interannual fluctuations probably related to changes in environmental factors (Millán, 1999; Petitgas et al., 2013). The peak occurred during the transition between the cold and winter mixing conditions and the warm and stratified summer water conditions (Motos, 1996). In this case, the negative and statistically significant correlation between the anchovy spawning peak and chlorophyll-a support the hypothesis that the spawning peak advances when the phytoplankton abundance increases, i.e. a bottom-up process influencing egg production. The phytoplankton abundance is directly related with zooplankton, a key trophic level for

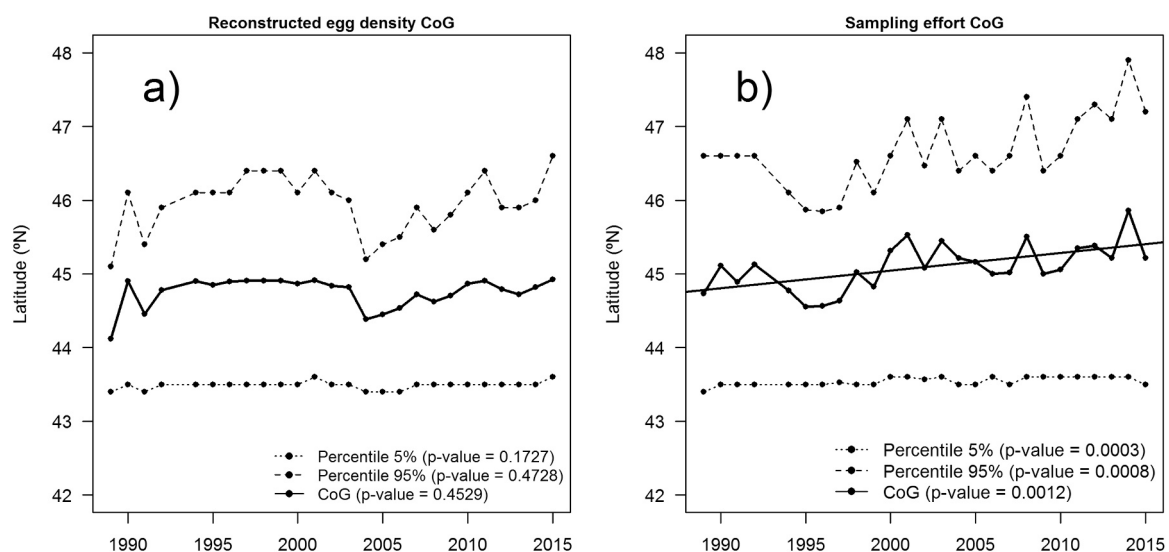


Fig. 8. Latitudinal shift of the a) reconstructed spawning distribution models Center of Gravity and percentiles 5 and 95 and b) sampling effort between 1989 and 2015.

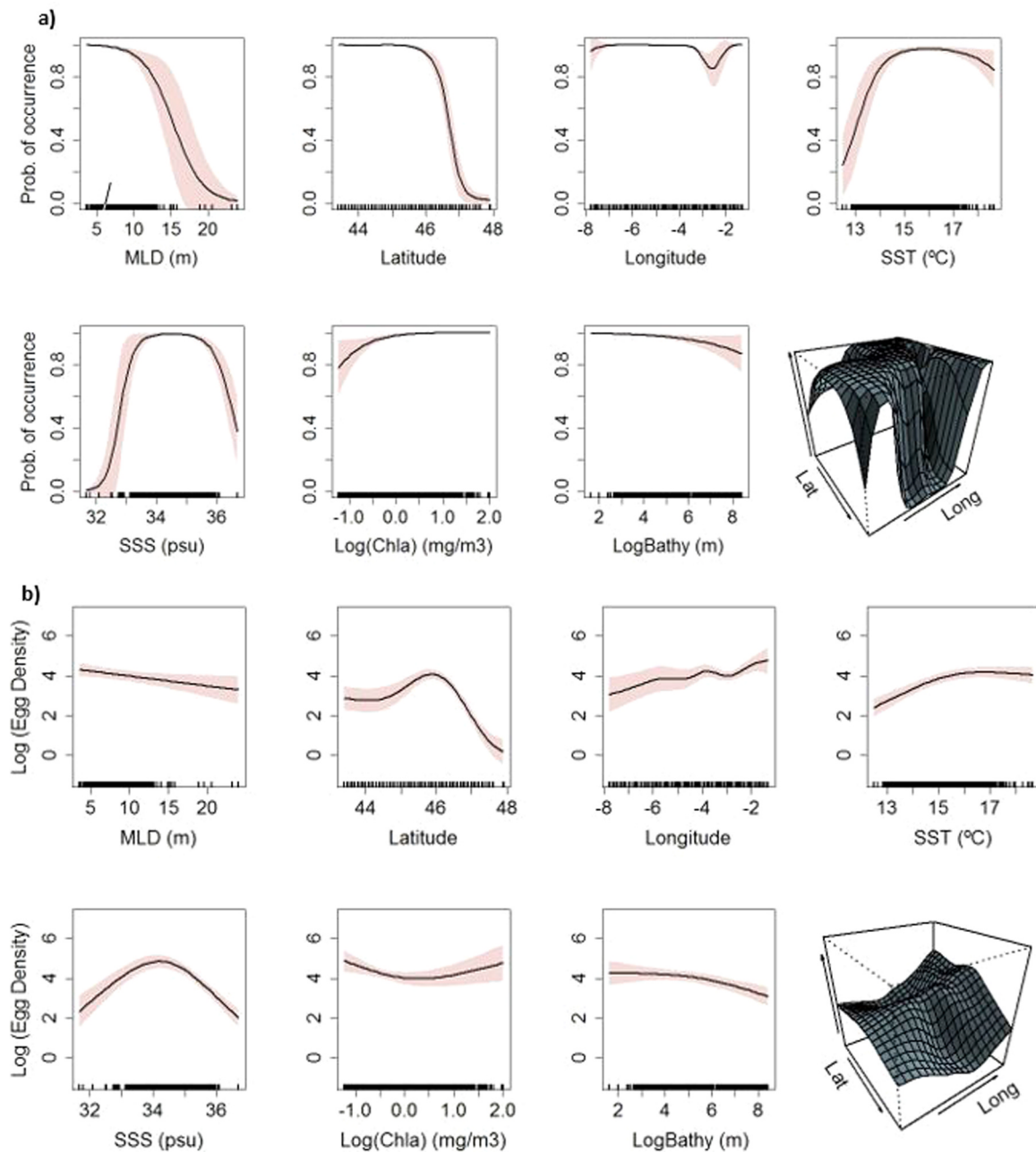


Fig. 10. a) Egg Presence/Absence (dev. expl. = 48.4%) and b) egg Log Density responses curves (dev. expl. = 58.1%) for MLD, Latitude, Longitude, SST, SSS, LogChla and LogBathy and relation between coordinates.

anchovy feeding. This result agrees with Somarakis et al. (2004) who associated earlier spawning peak with areas of high productivity and favorable adult feeding conditions. In other small pelagic species (i.e. mackerel), earlier spawning peak was found as a result of other variables such as temperature increase (Jansen and Gislason, 2011).

The high GSI interannual variability corresponds to large individual differences in gonad development. While the highest gonadal weights occurred during the spawning period, the lowest body weights were recorded towards the end of the spawning period (in autumn). This agrees with the studies carried out for anchovy in other areas. For European anchovy in the Bay of Cádiz, Millán (1999) found a more extended and delayed spawning peak (between June and August) and a resting period between November and February, while Regner (1996), reported July as the period of highest GSI for the Adriatic anchovy. The historical increase in GSI from 1989 to 2015 results from the significant increase in relative gonadal weight. Batch fecundity (the number of

viable eggs usually released by a serial spawner in a pulse of spawning) is linearly related to ovary free body weight (Santos et al., in press; Sanz and Uriarte, 1989). Instead, the idea of continued feeding during spawning period is suggested and energy requirement for spawning would then be satisfied by food intake (Dubreuil and Petitgas, 2009; Somarakis et al., 2004). Ovarian-weight is negatively affected by poor environmental conditions and it is reflected by a lower and fluctuating GSI (i.e. Millán, 1999). In the same manner, Motos (1996) stated that the spawning period peak coincides with maximum values of zooplankton biomass, which suggests that good conditions and food availability can increase gonadal weight and also influence batch fecundity along with spawning frequency (Hunter and Leong, 1981). This has been observed for Adriatic anchovy, where egg abundance fluctuates with primary production (Regner, 1996). Anchovies, sardines, and sprats are characterized by a high plasticity in their reproductive characteristics and have the ability to respond rapidly to environmental

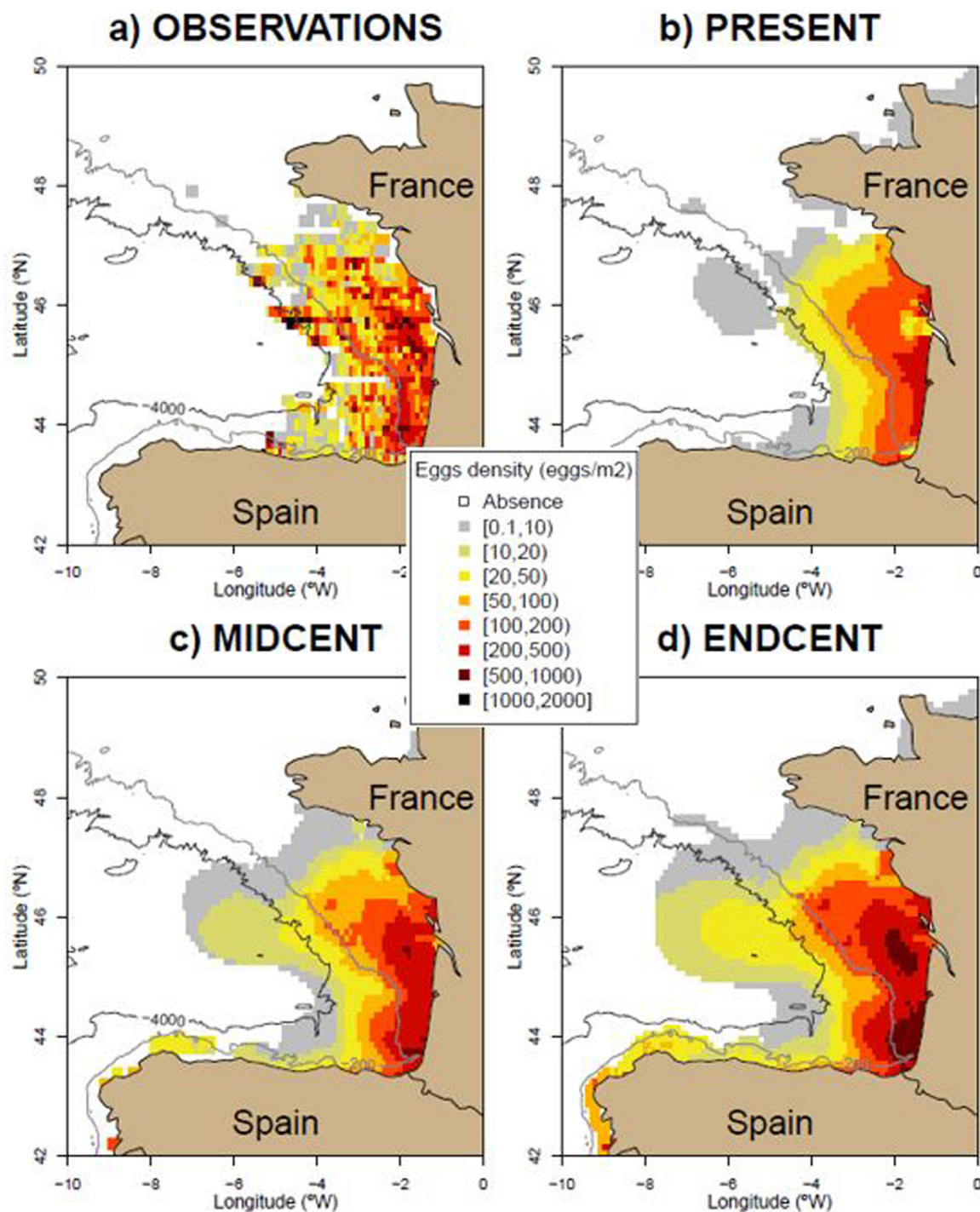


Fig. 11. Egg abundance models in the Bay of Biscay for a) observations, b) present habitat model (2002–2014), c) mid-century (2040–2059) and c) end-of-the-century (2080–2099). Variables selected in present model are: Latitude, Longitude, MLD, SSS, SST and Chl-a. Chl-a is not used in mid-and end-of-the-century models. 200 and 4000 m isobaths are also represented to see continental shelf slope.

changes (Alheit, 1989). Changes in fishing intensity could also affect phenology although the population was heavily fished before its collapse in 2005. The fishery was closed from 2005 to spring 2010 and no evidences of changes in phenology were found related to this event.

A high correlation was found between the latitude of the anchovy P95 and the total eggs. This supports the hypothesis that northern boundary variability is affected by the overall population (Somarakis et al., 2004). Due to interannual variability of the spawning dynamics, the area contracts or expands according to the overall size of Bay of

Biscay population, with eggs spreading over all the Bay in high abundance years (Santos et al., in press). As the basin hypothesis explains (MacCall, 1990), populations represent the optimal areas for reproduction, being restricted to more favorable spawning areas when the abundance is low. Conversely, fish tend to spread over a larger area when the biomass per area exceeds a threshold, in order to avoid intra-specific interactions (i.e. trophic competition and/or egg cannibalism) (Somarakis et al., 2004). Indeed, the northern limit of the egg distribution moved farther north in years when the egg production was

Table 3

All different model combination built with their deviance explained for Presence/Absence (PA) and log transformed density (logED), total anchovy egg abundance (eggs) in Bay of Biscay for different periods and change rate between mid- and end-of-the-century and present. Importance (SST) is the projected total anchovy egg abundance where the only variable which was changed for future values was SST and others were fixed to current values. The same for SSS and MLD.

Total egg production + s(Lat,Long)	PA (%)	LogED (%)	PRESENT	MIDCENT	FUTURE	Change rate Midcent	Change rate Future
All variables	48.0	57.8	80,076	125,984	211,854	1.57 ×	2.66 ×
Importance (SST)			80,076	88,341	114,341	1.10 ×	1.43 ×
Importance (SSS)			80,076	101,356	125,752	1.27 ×	1.57 ×
Importance (MLD)			80,076	84,241	86,935	1.05 ×	1.09 ×

higher. Bay of Biscay is limited by land in the east and south, so the eggs tend to expand to the west, but more to the north over the French continental shelf. In the future, the expansion of the distribution area will be probably be due to an expected increase in egg production.

4.2. Future projections of spawning activity

According to the RCP8.5 greenhouse gas emission scenario, substantial increases in anchovy egg density (or egg production) and spawning area are expected in the future. The total number of anchovy eggs in the BB is expected to be 2.66 times higher by the end-of-the-century compared with the present, with a 16.4% northwestward expansion of the spawning area due to geographical constraints imposed by the Cantabrian and the French coast in the south and east. A lesser increase in egg density (1.57 times), and expansion of spawning area (7.8%) are estimated by the mid-century as well. The implications of this to the geographic distribution of the Bay of Biscay anchovy population is that center of gravity will vary slightly and the direction is dependent of the time horizon considered. Such estimated increase in anchovy egg density is lower than, for instance, the interannual fluctuations of anchovy total egg production (which can vary by an order of magnitude, Fig. 7) (Alheit et al., 2010; ICES, 2016; Taboada and Anadón, 2015), but this variation is also influenced by fleet dynamic and management.

The expansion of the spawning area with a slight northward shift expected for the future, agrees with Ibaibarriaga et al. (2007), who predicted a northern expansion of the species distribution under climate change scenarios. Other studies conducted on a larger spatial scale (North Atlantic and Mediterranean Sea) obtained a substantial northward shift of the distribution of anchovy and a more extended anchovy potential habitat (Lenoir et al., 2011). This quantitative difference is hence due to the different areas analyzed, and the strong geographical attachment of the Bay of Biscay anchovy spawning to the coast and river plumes. Anchovy has a density dependence selection of the spawning area (Motos et al., 1996; Santos et al., in press). In years with high adult abundance, spawning occurred in most of the coastal area with higher intensity in the main river plumes but not all the potential oceanic area was occupied by larger and older anchovies. In years with low adult abundance, spawning is practically restricted to the principal spawning areas associated with the estuaries of Gironde, Adour and Bidasoa, in the southeast region of the Bay of Biscay. These places seem to form a refuge which maintains minimal sustaining conditions for this anchovy population even in adverse environmental conditions (Motos et al., 1996). The Bay of Biscay population is part of a species with a larger distribution range, and probably tolerate wider environmental ranges than those that are in the Bay of Biscay.

In a recent study conducted by Raybaud et al. (2017), an increase of the probability of the occurrence was expected in the northern area such as northwestern part of the Black Sea, Celtic Sea, English Channel, North Sea, the southern part of the Norwegian Sea and in the Bay of Biscay, hence, in agreement with our results. The study of Raybaud et al. (2017) was based on projecting occurrence probability of anchovy adults under SST change scenarios. Although our study is focused only on the Bay of Biscay, our model is based on different climatic changes

(not only SST) and provides egg density data collected in a yearly scientific survey (not only occurrence probability), which is important for fisheries management.

Projected changes in fisheries are more complex than simply northward shifts of species distributions, abundance changes or earlier spawning peaks (Brüge et al., 2016; Burrows et al., 2011). Egg abundance fluctuations are correlated with changes in temperature, salinity, primary production and zooplankton abundance, some of them with a one-year lag (Regner, 1996). Our results showed that not all environmental variables analyzed (sea temperature, salinity and mixed layer depth) affect future projections equally. However, when modeled one by one, all the variables result in an increase of egg abundance in the future.

Temperature, which interacts with other stressors operating at large scales, is considered the main force driving changes in marine ecosystems (Montero-Serra et al., 2015; Portner and Peck, 2010). However, in this study, the sea surface salinity was found to be the variable that results in a highest projected increase in anchovy egg abundance. It would be expected that the temperature window for anchovy eggs would remain tolerable (Ibaibarriaga et al., 2007) and possibly even more favorable.

Motos et al. (1996) hypothesized a link between anchovy presence and the freshwater runoff originating in river plumes, such as the Adour and Garonne rivers in the BB. However, the anchovy spawning habitat is found in a very wide salinity range, so it is more associated with coastal areas rather than with a given salinity (Reid, 1966). The Gironde estuary used to be an occasional spawning site in the past, but it has become a recurrent anchovy spawning center in the present (Bellier et al., 2007). The Loire river, which is located 250 km north of the Gironde and has the same freshwater discharge and seasonal dynamics, did not support any anchovy population in 1996 (Koutsikopoulos and Le Cann, 1996). Nevertheless, eggs have been recently found in BIOMAN surveys in this area (Santos et al., in press) and consequently, Loire river plume appears as a suitable zone to support high egg densities in both future models (mid- and end-of-the-century) and one-by-one-forced environmental variable models. In salinity-based model projections, total egg abundance is higher than temperature-based projections and most of the anchovy eggs are found in river plumes, thus the Loire is a likely candidate as an important spawning zone in the future.

MPIOM global model for future projections estimates freshwater inputs as the difference between precipitation and the sum of evaporation, river runoff and glacier melting (which most of the time is not taken into account). Precipitation is the only parameter which is simulated and river runoff is used as observed monthly mean of the largest 50 rivers of the world (Marsland et al., 2003). Considering only the most important rivers worldwide, the river runoff resolution might be low at local scale, hence the projections are not probably incorporating the salinity spatial heterogeneity in the BB due to precipitation differences at each basin.

Anchovy spawning is also related to the mixed layer depth such that a higher egg abundance is found in larger haline stratified conditions (shallow MLD) (Planque et al., 2007). River discharge increases the water column stratification, since freshwater decreases upper layer

density and suppresses mixing (Costoya et al., 2015). In our anchovy spawning habitat model, the mixed layer depth is used as a proxy of water column (haline and thermal) stratification. MLD-importance model projections are the lowest with an increase of 1.02 (1.05) times the present egg abundance in the mid- (end-) of-the-century. Global climate change models project the MLD to be 7 (12) m shallower due to ocean warming and subsequent water column stratification. Although the MLD decrease is mostly due to an increase in the water column temperature in the projections, the model is not able to distinguish it from the haline stratification although it could resemble freshening from changed river plume conditions. We assumed in our model that thermal mixed layer depth is a good representation of the mixed layer depth because SST explained slightly more MLD deviance (35.1%) than salinity (25.5%) and halocline and thermocline depth did not differ (Suppl. Info. Fig. 4a, b). There is a substantial stratification increase (MLD decrease) across the whole region that is larger in the open-ocean than in coastal zones and throughout the year (Holt et al., 2010). This could explain the larger projected expansion of anchovy eggs across the study area in the MLD-model than others. The same pattern was recorded in 2003, when a wide area was covered in spawn, which was related to the stronger stratification caused by an anomalously intense solar heating (Bellier et al., 2007).

These three variables (SST, SSS and MLD) are not the only ones controlling the spawning habitat. The multi-model average across 16 IPCC5 models shows up to a 30% decrease in primary and export production globally by the end of the 21st century with respect to the historical value (Cabré et al., 2014) although some specific areas such as the northern European Sea (the Barents Sea), the Baltic Sea and Black Sea, show an expected increase in primary production (3–15%) (Chust et al., 2014). Other studies project higher reductions in plankton biomass (reduce to less than a half, Schmittner, 2005) due to a decrease in the strength of the Atlantic Overturning Circulation (Collins et al., 2013; Meehl et al., 2007). However, zooplankton production is not expected to change proportionally to primary production, triggering changes in the trophic ratio (zooplankton biomass divided by phytoplankton biomass) in the future and a slight restructuring of the food web (Chust et al., 2014). Some latitudinal shifts are also expected. The copepod community is expected to shift poleward 8.7 km per decade on average, with a 12–13 day earlier phenological peak predicted by the end-of-the-century (Villarino et al., 2015). We built the model and projected under the climate change scenario (RCP8.5) assuming that the environmental variables that most affect anchovy spawning are SST, SSS and MLD. We did not include climatic multi-decadal variability drivers such as the North Atlantic Oscillation (NAO) or the Atlantic Multidecadal Oscillation (AMO) and other biological variables in our models and assumed that ecological relationships (inter- and intra-specific interactions) will remain similar in the future, which is a limitation of our projections. We also assume that changes in other physical drivers such as wind will be reflected in our model environmental variables. Furthermore, systematic differences in climate sensitivity and response between species or life-stages can desynchronize ecological interactions (Thackeray et al., 2016).

The small pelagic functional group has a keystone position in marine ecosystems and coastal economies worldwide due to its role to sustain both predators and fisheries directly and indirectly (Pikitch et al., 2014). In the past, studies focused on disentangling the effects due to climate from fishing pressure. Recently, the interest has shifted to the interaction between both drivers and the change in sensitivity (strength of the relation between biotic and climatic variables) (Macías et al., 2014). Climate-induced changes can collapse some stocks, particularly those that are in the southern edge of species distributions (Beaugrand et al., 2008). Brander (2007) suggested that a reduction of fishing mortality would decrease climate-induced impacts, because overfishing is probably acting in synergy with climate forcing. Climate change impacts could also be positive, increasing new fishery opportunities (Cheung et al., 2009; Hobday, 2010) as it is the case for the Bay

of Biscay anchovy, where this and other studies at larger geographical scales suggest that can be favored by recent trends in climate change.

General Circulation Models are able to represent many physical processes that drive large-scale climate change, but they are limited in their representation of coastal areas (Tinker et al., 2016). Downscaling data from global climate models to smaller areas (Holt et al., 2012) is hence crucial to obtain accurate climate projections at regional levels (Chust et al., 2014). Besides, ecological niche-based models have to be able to approach the complete curve of environmental predictors to be valid (Thuiller et al., 2004). With all these limitations, modelling the spawning habitat and spawning activity along with available environmental information and projections to the future could be the low-cost first step to designate potential spawning fish habitats (Schismenou et al., 2008).

5. Conclusions

This study showed that anchovy spawning peak advanced in a rate of 5.5 days/decade and a general increase of GSI from 1987 to 2015 in the Bay of Biscay. These changes might be associated to changes in phytoplankton abundance. Moreover, the spawning area expands/contracts depending on the total egg production during this period. Ocean warming and climate change effects are expected to intensify during the 21st century triggering an overall egg abundance increase and an expansion of the anchovy spawning distribution. Since the anchovy habitat is closely related to river plumes such as the Adour and Garonne, other large river mouths, such as Loire, might be colonized in the future. Our projections aim to inform the local fishing community and managers concerning future potential scenarios to develop management plans taking climate change into consideration. Our study suggests that climate change will increase the suitable spawning habitat and the egg production of anchovy in the Bay of Biscay and hence the anchovy population, although more research should focus on monitoring spawning trends, and exploring other potential drivers, adaptive strategies and phenology responses to reduce uncertainties in the projections.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr2.2018.07.007.

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